The influence of sluice gate operation on the migratory behaviour of Atlantic salmon *Salmo salar* (L.) smolts

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ABSTRACT

Numerous studies have examined the effects of high-head dams on salmonid smolt migration, but few have examined smolt behaviour at sluices managed to regulate water levels. We quantified passage success and time to passage of wild and hatchery origin juvenile (smolt) Atlantic salmon (*Salmo salar* L.) migration in relation to sluice operation (for water level and flood risk management) at Bala sluices on the upper River Dee, North Wales, including the occurrence of flow-reversal conditions from the Dee to Llyn Tegid (Lake Bala) immediately upstream. Ninety four smolts (67 wild, 27 hatchery origin) were caught, acoustic tagged, released at the capture site and tracked with a fixed receiver array in April to May 2015. Of the tagged fish, 91.5% successfully reached and passed the sluice gates. Of the tracked smolts that reached the sluices 6.6% failed to successfully migrate downstream through the sluices and 3.2% took over 4 days to pass. There was no significant difference in travel speed, nor the proportion successfully passing, between wild and hatchery reared fish. Smolts migrated quicker at higher flows. Smolts travelled at lower speeds through the sluices than the preceding section from which they originated, suggesting that migration may have been delayed by the sluice gates. Smolts passed through the sluice reach more quickly with higher discharge. Specifically, smolts moved quicker through the sluice reach when the aperture of the gate nearest the outside bend and thalweg increased, but the heights of the other gates did not significantly affect smolt speed past the structure. Flow reversal

episodes occurred only by day, whereas more smolt activity occurred by night (66.5% between dusk and dawn); under these conditions we found little evidence for loss of fish to the lake (three fish [3.2%] visited the lake and did not pass the sluices, but were last detected above the sluices), or contribution to delayed passage, as a result of flow reversal. It is concluded that at sites operating undershot sluices, where smolts migrate, upper water column orientated migration routes should be maximized where the thalweg hits the structure as this is likely to be the main route of transit adopted by smolts.

KEYWORDS: fish behaviour, smolt, flood risk management, sluice gates, migration delay, telemetry, flow reversal

1. INTRODUCTION

Rivers are considered to be amongst the most human-degraded ecosystems worldwide (Huckstorf *et al*., 2008). River modification has led to flow regulation, channelisation and habitat degradation which has impacted fish populations (Welcomme, 1994). The impacts of these interventions on fish communities include the reduced ability of fishes to exploit specialised habitats required for the completion of their life-cycle (Baras & Lucas, 2001). River regulation is considered one of the main causes for declines in river fish populations (Northcote, 1998; Lucas *et al*., 2009) and in-river barriers such as dams, sluices and weirs have a major role in the fragmentation of fluvial ecosystems (Poff *et al*., 1997; Kemp & O'Hanley, 2010). In-river obstacles not only impact fish populations by altering local habitat and restricting essential movement, they may also cause delays in migration and have the potential to cause physical damage to fishes, which can impact on fitness, if safe bypass routes are not available (Lucas & Batley, 1996; Aarestrup *et al.*, 1999; Coutant & Whitney, 2000; Hall *et al.*, 2011; Rolls, 2011). The severity of these effects of obstacles to migration depend on factors such as fish species, life stage, river hydrology and barrier type, and are thus likely to be highly site specific (Kemp & O'Hanley, 2010). Rehabilitation of riverine ecosystems in Europe is currently being driven by the Water Framework Directive (2000/60/EEC) and associated national policies. Thus free passage for migratory fish travelling between habitats essential for their life history, such as juvenile outmigration from natal areas and adult spawning migrations, is being addressed in this context.

The seaward migration of juvenile anadromous salmonids (smolts) is a crucial event in their life history. Smoltification is a period of great morphological, behavioural and physiological change when juvenile salmonids develop various adaptations that enable them to survive at sea (Thorstad *et al*., 2011a, 2012). Smolt survival is affected by a limited period of readiness (a physiological 'smolt window') and the timing of seawater entry with environmental conditions such as temperature, food, and predators (an ecological 'smolt window'). Physiological tolerance to full-strength seawater and anatomical adaptation to an open-water habitat is increased through a series of smolt characteristics developed in advance of seaward migration. These characteristics may regress if fish remain in freshwater, a process termed de-smoltification (McCormick *et al*., 1998), which may potentially be triggered by delays in migration. The migration corridor of smolts (mainstems of rivers and estuaries) is frequently impacted by pollution, dams, and other anthropogenic activities that may be directly lethal or increase mortality by delaying or inhibiting smolt migration (McCormick *et al*., 1998). Smolt migration tends to be surface orientated, especially in deeper water bodies (Johnson & Dauble, 2006). During migration, smolts are subject to elevated predation risks from mammalian, avian and fish predators (Aarestrup *et al*., 1999; Aarestrup & Koed, 2003). Delayed migration (Kemp & O'Hanley, 2010; Wright *et al*., 2014) and congregation of fish at structures can increase the potential for predation (Koed *et al*., 2002; Schilt, 2007) and energy expenditure (Osborne, 1961; Congleton *et al*., 2002), resulting in decreased fitness (Geen, 1975; McLaughlin *et al*., 2013) and survival (Raymond, 1979; McLaughlin *et al*., 2013). Thus such delays during this time-specific and vulnerable life history stage can potentially have large impacts on the survival of smolts and the health of salmonid populations as a whole.

A wide variety of river engineering structures exist which may affect the passage of salmonid smolts, from large dams and hydropower with a range of potential routes (Raymond 1979; Coutant & Whitney, 2000; Schilt, 2007; Calles & Greenberg, 2009) to simple overflowing low-head weirs (Gauld *et al*., 2013). A common form of river engineering is the occurrence of sluice gates for flow control. Sluice gates create complex hydraulic conditions for approaching flows and their nature varies with sluice gate design (undershot or overshot, with some flow via a fixed aperture), and may alter with changing discharge conditions and operating regimes, resulting in behavioural modifications to downstream migrating fish approaching such devices (Piper *et al*., 2015). A common feature of flows at sluice structures and surface bypass collectors is a rapidly accelerating flow field as water approaches the opening, often causing alteration of behaviour of downstream-migrating fish approaching the structure and frequently causing rejection of entrance and delaying passage (Haro *et al*., 1998; Kemp *et al*., 2008;

Enders *et al*., 2009). Often sluice management is directed towards multiple demands concerning flood protection, transport of stored water, recreational use and for meeting hydrobiological needs. This can generate unnatural hydrological conditions, such as flow reversal, when water delivery exceeds controlled sluice capacity in a low-gradient river reach. The aim of this study was to ascertain the local impacts of flow-control sluices on the behaviour and survival of Atlantic salmon *Salmo salar* (L.) smolts and to consider how passage impacts might be minimised.

The study adopted a field experimental approach employing an existing set of sluices constructed for flow regulation associated with water storage reservoir management and flood defence. Our approach was not to alter the sluice management regime as we wanted to measure responses under normal operational management regimes. As such, our study is correlative but quantitative. The site chosen was typical of the type characterizing many rivers where water resources must be managed alongside formal conservation status objectives.

2. MATERIALS AND METHODS

2.1 Study area

The study site centred on Bala Sluices (52.9070N, -03.5834W), 15.5 km from the source and 95 km upstream of the tidal limit, on the upper River Dee, North Wales, immediately downstream of the confluence with the Afon Tryweryn tributary (Fig. 1). The sluice system at the outlet of Llyn Tegid (Lake Bala) and the releases from Llyn Celyn, are managed by Natural Resources Wales (NRW) to regulate the flow of the River Dee, North Wales, to reduce flood risk, support downstream abstraction through managed releases and to maintain a summer water level for recreation in Llyn Tegid itself. Flow regulation at the Bala sluice gates also limits the influence on downstream river levels in the main River Dee of the Llyn Celyn reservoir releases, that usually occur during the day as opposed to night, and thus facilitate watersports at the national whitewater rafting center on the Afon Tryweryn tributary. Additional water contributing to the Afon Tryweryn is derived from the 112 km^2 Afon Tryweryn catchment. The sluice gates are operated via a semi-remote control system and depending on flow conditions and the water level in Llyn Tegid, water can flow either out from the lake exit (typical condition) or back into the lake (less frequent). If more water is being supplied by the Afon Tryweryn tributary (either reservoir release or natural run-off) than is allowed to flow down the Dee due to the

sluice gates' mode of operation, this can cause the River Dee to back-up, or flow into the lake's outflow. This phenomenon is known as 'flow reversal'. This typically occurs as a result of two primary causes. Firstly, water release from LLyn Celyn occurring at a rate greater than the outflow from Llyn Tegid; and secondly a flood event on the Tryweryn when discharges at Bala sluices are reduced to mitigate flood risk along the River Dee corridor.

The Dee and Llyn Tegid are designated a Natura 2000 Special Area of Conservation (SAC), with Atlantic salmon a primary feature, under the EU Habitats Directive. The Dee is also an Index River for Atlantic salmon stocks (CEFAS, 2014) but has been 'at risk' / 'probably at risk' of failure to meet conservation targets for salmon stocks since 2010 and is projected to do so to at least 2019 (Ian Davidson, NRW, pers. comm.), reflecting the 'unfavourable condition' status of the salmon population in the context of the SAC. No fish pass exists at Llyn Celyn dam and hatchery-reared juvenile salmon from Dee broodstock have been stocked annually, as parr and fry, in the Tryweryn since construction of Llyn Celyn, as a mitigation for the loss of upstream habitats, although alternative mitigations are being explored and the stocking of hatchery reared fish being phased out.

Bala sluices extend across the full 35 m width of the Dee. Looking downstream towards the structure there are six sluice gates (five visible; Fig. 2). From the left, operationally the gates are numbered as follows; 1 (first from true left bank), 2 (second from left-hand bank), 5 (middle upstream), 6 (middle downstream), 3 (second from right hand bank) and 4 (first from right hand bank). Gates 1-4 are undershot guillotine gates and offer migrating smolts a transit route that is not surface orientated, unless they are lifted clear of the water's surface. Gates 5 and 6 are remnants of an old fish lock at the structure. Gate 6 (downstream) is an undershot gate with a penstock opening that creates an overshot situation when Gate 6 is "closed". Gate 5 (upstream) allows flow into the fish lock by means of a penstock opening in the main structure and up to lake levels of 2.3 m (Upper Dee Flood Alert) this is the only opening that would operate. Above 2.3m, Gate 5 is wound down and water flows over a v-notch weir in its top plate and also through the penstock opening (Steve Mayall, NRW, pers. comm.).

The natural thalweg of the Dee upstream of the sluices runs down the left bank as it approaches the sluices along the outside of the bend. However, at low flows when gate 5 is opened exclusively, flow offtake occurs in the middle part of the sluice structure. As discharge arriving at the sluice increases, and

upstream water level increases, sluices 1 and 2, on the left bank, in the vicinity of the natural thalweg, are opened relatively more than sluices 3 and 4.

2.2 Environmental Data

River flow was gauged at 'Weir X' (immediately downstream of receiver array 2, Fig. 1) on the Tryweryn and also at Bala Gauging Weir and ultrasonic station (immediately downstream of the receiver array 6, Fig. 1) on the Dee. Periods of flow reversal were identified and the flow rate upstream of the structure were calculated by calculating the difference in the gauged flow at 'Weir X' and Bala Gauging Station, when the former exceeded the latter, with positive values representing 'normal' downstream flows and negative values representing flow reversals. Sluice gate heights were measured and recorded every fifteen minutes by NRW telemetry systems. Water temperature (°C) was measured hourly at two points on the Tryweryn (both at receiver array 2: Fig. 1) from 9th April to 16th June 2015 (Aquatic 2 logger, TinyTag; Gemini Data Loggers UK Ltd., Chichester, UK) and a mean value calculated and used as an approximation of water temperature within the ~4km study reach over the study period.

2.3 Fish capture, tagging and tracking

Smolts were caught by 3 fyke nets (4.5m wings leading to 7 hoops [470-970mm diameter], mesh size was 15mm on the wings and for the first 3 hoops reducing to 10mm for the final 4 hops) set, to cover the vast majority of the width of the channel, in the Tryweryn, 600 m upstream of Weir X (Fig. 1) in the evening and early night. The fyke nets were specially adapted with 3m long 'cod ends' (approx. 500mm diameter) constructed from fish friendly 'carp sack' material (with approx. 1mm diameter holes) to reduce the possibility of physical damage and scale loss which could influence subsequent behaviour/survival; pilot trials confirmed the effectiveness of these. Fyke nets were set at night only. Smolts originating from stocked hatchery fish were identified by adipose fin clip. In total ninety-four salmon smolts (67 wild and 27 of hatchery origin), from a much larger number caught, were tagged over fourteen nights between 16th April and 21st May 2015. Emphasis was put on tagging wild fish, as hatchery reared stocking is being phased out in the River Dee catchment. Fish were selected for tagging based on their size (≥120mm) and availability; the aim was to tag approximately eight fish per trapping night to trickle fish through the array throughout the migration season to represent a variety of different flow scenarios. The size range tagged (mean ± SD [range] fork length, 136.0 ± 9.5 mm [120–165 mm])

reflected all but the smallest (100-119 mm) salmon smolts migrating through the reach. Vemco (Nova Scotia, Canada) V5-180kHz coded acoustic tags (cylindrical, 12 mm long by 5 mm diameter; mass in air, 0.65 g) with nominal code delay of 20 s and an operational life of 22 days were used. Tags were implanted into the body cavity, licensed under the Animals (Scientific Procedures) Act 1986, using a method similar to that described by Gardner *et al*. (2015). Using body mass estimated from a standard length-mass relationship for Atlantic salmon smolts from Flanagan *et al.* (2006) mean ± SD (range) tag burden was 2.6 ± 0.48 % (1.46-3.65 %). Although the evidence that larger tag burdens may impact small salmonids is equivocal (Brown *et al.*, 1999; Newton *et al*., 2016) we consider minimization of possible tag effects, including tag burden, to be desirable in seeking to ensure that behaviour and survival of an unbiased sample of tagged fish is as natural as possible (Cooke *et al*., 2012). Fish were anaesthetised using 2-Phenoxy ethanol (0.4 ml l^{-1}), and their fork length (mm) recorded. The disinfected coded acoustic tag was implanted into the peritoneal cavity through a small incision which was closed with a single suture (VICRYL™ undyed braided absorbable W9520; Ethicon, Piscataway, NJ, USA). Once the procedure was complete, fish were placed into a recovery tank filled with highly aerated water to ensure complete recovery from anaesthesia. Fish were then retained for a further 30 minutes of observation in in-river tanks before release, which was usually approx. 1-2 hour after capture. Crucially, as smolts tend to group together as an anti-predator tactic, small groups of tagged fish were released within larger groups of untagged smolts, also temporarily retained (Gauld *et al*., 2013), in the same in-river tanks, to replicate this natural shoaling behavior and afford the tagged fish some initial 'safety in numbers' protection.

Twenty automatic datalogging receivers with omnidirectional hydrophones (VR2W-180kHz, Vemco, Nova Scotia, Canada) were used to record the presence of tagged fish continuously within range of the receivers. These were arranged to form six discrete receiver arrays (Fig. 1). Three receivers per array were positioned mid-channel when channel width was <30 m, and four receivers per array were used when channel width was >30 m, positioned in river margins, two receivers per bankside. Receivers were spaced 40 m apart within each array to ensure maximum detection (giving a detection zone of at least ~80-120 m, providing multiple detection opportunities for tag code emissions during transit, even at high fish speeds), confirmed by multiple range tests during three different water conditions (low reservoir release, high reservoir release and flood). Subsequent analysis of fish known to have passed arrays (due to detection further through the receiver system) revealed array detection efficiencies of 100% for arrays 2 and 5 and 88.4% at array 3 potentially due to the shorter detection reach here and

background noise from a nearby fish pass. Mobile tracking was carried out with a VR100-180kHz (Vemco, Nova Scotia, Canada) and an omnidirectional hydrophone on one occasion (28/05/15 - 7 days after the last fish was tagged), to search the entire study area, by boat, for any tags still present. The fate of each tagged fish was established dependent on their last detection at a specific array. For example, if a tag was last detected at array 6 (downstream of the sluices) it was assumed to have safely navigated the study area and continued its migration seawards. If a tag was last detected at an array other than those at potential exits to the study area (*i.e.* arrays 1, 4 and 6) it was assumed to have died (either by predation or post-tagging mortality; tag failure and tag expulsion were assumed to be zero, but see Discussion for further consideration) within the study area. Mortality rates for both the control and sluice reaches were calculated per km, to standardize for small differences in reach distance and to facilitate comparison with the published literature. To assess diel activity within the study area, a frequency distribution of the combined smolt arrival times at arrays 3, 5 and 6, as the main outward migration route, was constructed.

2.4 Data handling and statistical analysis

Detections from each individual receiver were grouped by array. The distance (m) of each array centre point from the sluice gates was measured using ArcMap (ESRI Ltd, Redlands, CA, USA) allowing the movements of each fish to be calculated. To aid interpretation of the influence of the sluices on the movements of smolts, the speed of each tracked fish was calculated for two reaches of the study area, a control reach (between array 2 and 3) and a reach containing the sluice gates (between array 5 and 6). The control reach was not a totally natural reach, containing two low head weirs, 'Weir X' an NRW gauging weir described above and 'Weir Y' which contained a centrally located Larinier fish pass to facilitate the upstream passage of adult salmonids. However, it contained slack-water 'holding' habitat, as well as glide and riffle, and natural bed material (as did the area upstream of the sluices). Due to the presence of cross-channel weirs, the control reach may have been expected to inhibit downstream smolt movement as found by Gauld *et al.* (2013); thus comparison of speed of passage through these two reaches is a conservative one for evaluating potential delay effects of the sluices. Data were tested for normality (Anderson-Darling test) and homogeneity of variances (Bartlett test). Speeds for individual fish in both reaches (for all fish, just wild fish and just hatchery fish) were analysed with Wilcoxon rank sum tests because data were not normally distributed. Differences in speeds between fish of wild and hatchery origins through the control and sluice reaches were also tested with Wilcoxon rank sum tests.

General Linear Model ANOVAs were used to investigate factors influencing speeds through each reach; factors included in the analysis were Tryweryn temperature, flow (at 'Weir X' for control reach and upstream of the sluice structure for the sluice reach) and fish origin (wild/hatchery). The relationship between smolt speeds through the sluices reach and individual gate height were also analysed with General Linear Model ANOVAs. Potential differences in the mortality of wild vs hatchery fish were analysed with 2-sample test for equality of proportions with continuity correction, and the diel pattern of smolt activity were analysed with Pearson's Chi-squared test with Yates' continuity correction. All models were conducted using the aov function in R version 3.03.

3. RESULTS

3.1 Smolt capture and tracking

All salmon smolts caught and those tagged were displaying physical and behavioural characteristics consistent with fully developed smolts, having silver body colouration and being caught by a method that targets fish which are actively migrating downstream (Wedemeyer *et al*., 1980). Salmon smolts of hatchery origin were the dominant catch (n = 710, 86%), with the capture of wild salmon smolts (n = 112, 14%) being sporadic. A large catch was made during a single night (5th May 2015) following a rainfall event, thus 54% of the tagged wild smolts were tagged on this single night.

The 94 tagged fish took on average 22 hours (range: 32 mins to 14 days) to continue migration (first detection at array 2) after release. Three of the tagged smolts were recaptured in the fyke nets at 0, 2 and 5 days post tagging. The fish recaptured 5 days post tagging displayed a clean, closed incision site, with the suture (and thus tag) still present. Out of 94 smolts tracked (67 wild, 27 hatchery), 91 reached the sluice gates. Of these, 85 (91.5%; 61 wild [91.0% of the wild fish], 24 hatchery [88.9% of the hatchery fish]) successfully passed the sluice gates. There was no significant difference between the proportion of wild nor hatchery fish that successfully passed the sluice gates (equality of proportions; X^2 = 0.212, df = 1, P = 0.644). Three tagged salmon (3.2%; 1 wild, 2 hatchery) were detected at the exit to lake Bala; none of these three fish went on to pass the sluices, but all were last detected at or near the sluices (thus they were not lost in the lake). Six (6.6%; 4 wild, 2 hatchery) of the 91 tracked smolts that reached the sluices, including the three that visited the lake, failed to successfully transit the sluices. Mortality rate within the control reach was calculated as 6.7% km^{-1} compared with 11.2% km^{-1} within the sluice

reach. Three fish (3.2%; 2 wild, 1 hatchery) experienced a time to passage exceeding 4 days at the sluice gates. Only two smolts exited the Tryweryn while flow reversal was occurring; both successfully navigated the sluice gates. Times to passage associated with these fish were seven hours eleven minutes (speed of 0.02 m s^{-1}) and three hours thirty-five minutes (speed of 0.04 m s^{-1}) respectively. During the mobile tracking / manual search of the study area on 28 May 2015, four tags were located. One of these tagged fish went on to successfully migrate through the sluices on 1 June 2015, the remaining three fish (3.2%; 2 wild, 1 hatchery) were assumed to represent mortalities within the study reach.

Mean time of passage through the control reach was 87.5 minutes (range: 8.0 to 1209 minutes) which equates to 0.06 days (range: <0.01 to 0.8 days). Compared with a mean time of passage through the sluice reach of 588.1 minutes (range: 9.0 to 11101.0 minutes) which equates to 0.4 days (range: <0.01 to 7.7 days). Frequency distributions for the speeds of individual smolts through the control reach and sluice reach ((Fig. 3); demonstrate a distinct bimodality for the control reach. The speed over ground of individual smolts tracked through the control (median = 0.27 m s^{-1}, [range: 0.01 to 0.99 m s^{-1}] interquartile range [IQR]: 0.46 m s^{-1}) and sluice (median = 0.20 m s^{-1}, [range: <0.01 to 1.09 m s^{-1}] IQR: 0.43 m s^{-1}) reaches were significantly different for all fish (Wilcoxon rank sum test, W = 3561, df = 75, P = 0.013; Fig. 4) and wild fish only (control median = 0.25 m s^{-1}, IQR: 0.50 m s^{-1}, sluice median = 0.11 m s^{-1}, IQR: 0.43 m s^{-1}; Wilcoxon rank sum test, W = 1831, df = 52, P = 0.007) with smolts travelling at lower speeds through the sluice reach than the control, indicating that smolts were delayed, relatively, by the sluice gates. Speeds of individual hatchery smolts only, tracked through the two reaches were not significantly different (control median = 0.34 m s^{-1}, IQR: 0.46 m s^{-1}, sluice median = 0.29 m s^{-1}, IQR: 0.25 m s^{-1}; Wilcoxon rank sum test, W = 293, df = 23, P = 0.538). However, hatchery smolts were slower through the sluices reach than the control and the non-significance may reflect the smaller sample size. There was also no significant difference between the speeds of wild and hatchery origin fish in the control reach (Wilcoxon rank sum test, $W_{53,23}$ = 618, P = 0.9279) nor the sluice reach (Wilcoxon srank sum test, $W_{53,23}$ = 492, P = 0.1858).

A General Linear Model ANOVA revealed no significant effect of fish origin (GLM ANOVA; $F_{1,76}$ = 0.216, P = 0.643), temperature (GLM ANOVA; $F_{1,76}$ = 1.103, P = 0.297), nor fish length (GLM ANOVA; $F_{1,76}$ = 0.012, P = 0.914) on speed through the control reach. However, there was a significant effect of flow (GLM ANOVA; $F_{1,76}$ = 28.717, P < 0.001), on the speeds of fish through the control reach. Similarly, a General Linear Model ANOVA revealed no significant effect of fish origin (GLM ANOVA; $F_{1,76}$ = 1.118, P = 0.293),

temperature (GLM ANOVA; $F_{1,76} = 0.003$, $P = 0.956$), nor fish length (GLM ANOVA; $F_{1,76} = 0.114$, $P = 0.736$) on speed through the sluice reach. However, there was again a significant effect of flow (GLM ANOVA; $F_{1,76} = 12.643$, $P < 0.001$), on the speeds of fish through the sluice reach. Thus the speeds at which smolts travelled through both reaches were independent of all variables with the exception of flow rate, with smolts moving quicker at higher flows.

A General Linear Model ANOVA revealed a significant effect of the height of gate 1 only (GLM ANOVA; $F_{1,76} = 14.191$, $P < 0.001$), with the heights of gate 2 (GLM ANOVA; $F_{1,76} = 0.901$, $P = 0.345$), gate 3 (GLM ANOVA; $F_{1,76} = 0.702$, $P = 0.404$), gate 4 (GLM ANOVA; $F_{1,76} = 1.154$, $P = 0.286$), gate 5 (GLM ANOVA; $F_{1,76} = 0.037$, $P = 0.848$), gate 6 (GLM ANOVA; $F_{1,76} = 0.071$, $P = 0.790$) having no additional significant effect on measured transit speed through the sluices reach. However, for GLM ANOVA, inputted parameters for testing should be independent of one another and gates 1 and 2 are known to operate in tandem. Thus the modelling was repeated with gates 2 and 6 omitted revealing a significant effect of gate 1 only again (GLM ANOVA; $F_{1,76} = 14.483$, $P < 0.001$); with gates 1 and 6 omitted revealing a significant effect of gate 2 only (GLM ANOVA; $F_{1,76} = 14.294$, $P < 0.001$) and with gates 1 and 2 omitted revealing a significant effect of gate 6 only (GLM ANOVA; $F_{1,76} = 4.333$, $P < 0.05$). Thus smolts moved quicker through the sluices reach when the aperture of gates 1, 2 and 6 increased, but the heights of the other gates did not significantly affect smolt speed across the structure.

To assess diel activity within the study reach, frequency distribution of smolt arrival times at arrays 3, 5 and 6 combined ($n = 257$), the main outward migration route, were produced (Fig 5). Smolts tended to be more active within the study area during the night time (Chi Squared; $X^2 = 13.78$, df = 1, $P < 0.0001$) with 66.5% of arrivals occurring during the hours of darkness (20:00-05:00) compared with 33.5% of arrivals occurring during day light hours (05:00-20:00), with an apparent avoidance of dawn and dusk.

3.2 Environmental data and sluice gate operation

The river remained low for the first two weeks of the study period (Fig. 6). Small amounts of rain at the end of April 2015 caused the river to rise for a short period (<24 hours). More substantial quantities of rain fell in the first week of May, the third week of May and the first week of June, resulting in more sustained periods (7-10 days) of elevated flows. Flow reversal occurred on 39 occasions over the period 1 March to 31 May 2015. Mean reversed flow was 4.2 m^3s^{-1}, and mean duration of flow reversal period

was 7.22 h, giving a total period of 281.75 h. All of these events occurred during daylight hours, usually being associated with reservoir releases from Llyn Celyn. Sluice gate operation during the study period was related to the rainfall events outlined above. At the beginning of the study, gates 1-4 were closed and gate 5 open, allowing a surface orientated migration route. During the three main rainfall events gates 1, 2, 3 and 4 were opened to varying degrees to allow increased flow through the structure. Gates 1 and 2 were operated simultaneously and more frequently during the second and third high flow events. Gate 6 (downstream center gate) was also raised during these events, to match the downstream water level which would have been elevated.

4. DISCUSSION

4.1 Smolt tracking

Survival through the immediate sluice zone under the flow regime studied was high, although the study area was only over a short distance, when compared to the total migration distance in the Dee (95 km from study site, with a further six substantial obstacles). Passage speed through the sluice reach was significantly slower, than through the control reach, for wild smolts but not for hatchery smolts, potentially due to a reduced sample size of the latter, since GLM showed no significant effect of origin on recorded speed. The significant difference is likely to reflect a genuine delay, since the 'control' section had obstacles too and contained deep, slower 'holding' areas. Smolts tended to be actively migrating predominantly during the hours of darkness, although some daytime migration was observed, with an apparent avoidance of dawn and dusk, in line with the findings of Ibbotson *et al*., (2006).

River flow significantly affected the speed of smolts through the control reach, which should be expected as smolts migrate downstream, and thus are likely to migrate faster, in elevated flows. The mean speed over ground of individual smolts tracked through the control reach was 0.34 m s^{-1} (range: 0.01 to 0.99 m s^{-1}), which falls within the range of literature values for Atlantic salmon smolts, which include 0.46 m s^{-1} (Rivinoja *et al*., 2004), 0.14 m s^{-1} (Martin *et al.,* 2009), 0.10 m s^{-1} (Davidsen *et al.*, 2009) and 0.02 m s^{-1} (Thorstad *et al.*, 2011b), giving a mean literature value of 0.18 m s^{-1}. Although downstream migration is not passive, smolts migrate in the main flow of the river with the highest water velocities and thus migration speed is dependent on the speed of the river flow. This is likely to explain the variation in literature values. The mean speed of smolts tracked through the sluice reach was 0.29 m

s^{-1} (range: <0.01 to 1.09 m s^{-1}), again within the range of the literature values cited above. Thus while the sluice structure may have delayed the smolts in comparison to the control reach, speeds through the sluice reach were still within those that could normally be expected in the wild in unmodified reaches. The distinct bimodality in transit speed through the control reach was likely a result of varying environmental conditions, particularly flow, affecting the speed of passage, as indicated by the GLM analysis.

Six of the 91 (6.6%) tracked smolts that reached the sluices failed to be detected at acoustic array 6, 590 m downstream. Assuming that these tagged smolts did not pass array 6 undetected (tagged smolt detection efficiency at site 2, 100%, site 3, 88.4%, site 5, 100%), they are believed to have died, as successful desmoltification and subsequent delayed outmigration in Atlantic salmon smolts in Britain is believed to be rare (Hogasen, 1998). Mobile tracking on 28th May 2015 located three of these tags in stationary positions in the Dee upstream of the sluices, having last been recorded moving between 2 and 6 weeks previously. These most likely represent mortalities as expulsion of implanted acoustic tags in smolts is rare and usually takes place over a longer time period (see Moore *et al.*, 1990). It is unlikely that the remaining tags detected at array 5, but not array 6, failed, since reported failure rates by Vemco are less than 2% (Vemco, pers. comm.).

A recent review by Thorstad *et al.* (2012) summarised natural smolt mortality rates (mortality occurring without links or associations with anthropogenic stress) during downstream freshwater migration as 0.3 - 7.0% (mean 2.3%) km^{-1}. The mortality rate experienced in the sluice reach during this study equates to 11.2% km^{-1} which is well above the mean mortality figure cited above and above the upper end of the range of values, assuming no tag failure and 100% tag detection at array 6. Compared with a mortality rate of 6.7% km^{-1} for the control reach. Thus the sluices may negatively influence the mortality rate of migrating smolts, outside the range of levels that could be experienced naturally. Given that the study area is in the upper catchment, there also exists potential for multiplicative effects from other barriers downstream to further increase mortality (Norrgård *et al*., 2013).

The maximum delay observed at the sluices was over seven days (equating to a transit speed of 0.00089 m s^{-1}). Delays of this magnitude at a single barrier may have the potential to increase predation rates (Aarestrup *et al*., 2009; Aarestrup & Koed, 2003; Jepsen *et al*., 1998; Gauld *et al.*, 2013) and cumulative effects from such delays at a number of barriers may have the potential to delay smolts to the point

where they miss their physiological window for successful saltwater entry. The length of this physiological window has been estimated at 313 D° (degree days; Urke *et al*., 2014a), 280-350 D° at 10-12°C (Stefansson *et al*., 1998) and 250 D° at 8.9-12°C for two strains of hatchery reared smolts (Handeland *et al*., 2004) and 328 D° (Urke *et al*., 2014b) for wild fish from River Stjordalselva, Norway. Urke *et al.'*s (2014b) findings for wild smolts equate to a window of approximately 27 days (at 12 °C). At Bala, 6.6% of tagged smolts failed to pass the sluices and a further 3.2% of tagged smolts took longer than 4 days to pass. Given that below Bala sluices there are a further six substantial obstacles over 95 km to the tidal limit, we regard a time from sluice approach to passage of 4 days, as a severe delay. It is not known how far through this physiological window the tracked smolts used in this study were, when they were tagged, however as the tagged fish were displaying the physical and behavioural adaptations associated with smoltification (*i.e.* silver body colouration and migratory behaviour) it has to be assumed that they were past, but perhaps close to, the beginning of this window. Peak hypo-osmotic regulatory capability is generally thought to coincide with smolt migratory behaviour, however some populations of anadromous salmonids may initiate migration early, potentially before they are able to adapt to full strength seawater (Clarke & Blackburn, 1977; Wedemeyer *et al.*, 1980). How long fish have been adapted before capture would depend on how far they had travelled from upstream to the capture site and how long they took to initiate migratory behaviour once adapted. Whether smolts delayed beyond this window would in fact die upon saltwater entry is uncertain and no study has yet demonstrated increased mortality of smolts upon saltwater entry due to delays at anthropogenic barriers. Smolts which have desmoltified in freshwater (Clarke & Blackburn, 1977) can still tolerate saltwater but are subject to physiological consequences, such as lower marine growth and survival (Virtanen *et al*., 1991; Staurnes *et al*., 1993; McCormick *et al*., 1998; Stefansson *et al*., 2008; Stefansson *et al*., 2012; Urke *et al*., 2014b). However, they could also possibly be expected to show an avoidance reaction to salinity and remain in the lower river longer than normal (Wedemeyer *et al*., 1980).

Tagging 54% of the sample of wild smolts during one peak night was sub-optimal in terms of experimental design. It may have been better to tag fish evenly throughout the study period so data could be representative of all likely flow conditions throughout the study period. However, fish were tagged when they could be caught and this may be more representative of the natural situation, as simultaneous migration is also an effective predator evasion strategy and is a usual occurrence on the River Dee (Ian Davidson, NRW, pers. comm.).

4.2 Influence of sluice operation and flow reversal

Salmonid smolts appear to follow the route of main river discharge (Rivinoja, 2005; Fjeldstad *et al*., 2012) thus routes that pass large volumes of water are also likely to attract a greater proportion of smolts. However, juvenile salmonids typically also migrate in the upper part of the water column, possibly an adaptation to use the part of the water channel with the highest water velocities (Davidsen *et a*l., 2005; Thorstad *et al*., 2012) which are usually found to occur from the surface to one-third of the depth of the channel, near the thalweg (Coutant & Whitney, 2000; Thorstad *et al*., 2012). Thus if passage routes in the upper water column are not available, relatively small or difficult to locate *e.g.* positioned perpendicular to the main channel, then smolts are likely to take longer to locate these passage routes (Johnson & Dauble, 2006; Fjeldstad *et al*., 2012) and thus increase associated migration delays. The significant effects of gates 1 and 2 on the speeds of smolts through the sluice reach are consistent with this, as these gates are positioned on the true left-hand side of the structure where the thalweg hits the sluices and were operated most often during elevated flow events *i.e.* when smolts tend to migrate. The significant effect of gate 6 is likely due to it being raised to match downstream water levels, thus during periods of high discharge when smolts are likely to migrate.

None of the three smolts that were detected at the lake exit went on to successfully pass the sluices. Although the sample size here is very low, this does suggest that smolts which do not navigate directly towards the sluice structure may be more prone to mortality (particularly predation) than those which do. These smolts did not appear to have initially been 'pushed' towards the lake by flow reversal. However, the influence of flow reversal may have contributed to their failure to safely navigate the sluices as they were all in its sphere of influence when reversal events occurred. While acknowledging the low sample size here, this does suggest that smolts which are caught up in such a phenomenon and move to the lake as a consequence, are likely to experience higher mortality than would otherwise be expected. Only two smolts exited the Tryweryn while flow reversal was occurring; neither of these fish moved towards the lake and both successfully navigated the sluice gates. The low number of fish exiting the Tryweryn during this phenomenon was due to the tendency of the tracked fish to be more active during the night time, as demonstrated by the array arrival time analyses. Atlantic salmon smolts exhibit a nocturnal migration bias early in the migration period when water temperatures are below 12 °C, later becoming increasingly diurnal (towards an equal day night split), when water temperatures are above 12 °C, but showing an avoidance of dawn and dusk, when predators are likely to be most active

(Ibbotson *et al*., 2006), also evident in our data. Whereas flow reversals usually occurred during day light hours, commonly associated with reservoir daytime releases from Llyn Celyn. Thus daytime flow reversal coupled with the dominant nocturnal migration pattern of salmon smolts (Ibbotson *et al.*, 2006; Thorstad *et al.*, 2012) were likely to help minimise negative effects due to flow reversal. However, the potential for flow reversal induced effects on migrating smolts could increase during the later migration period, when smolt movements could be expected to be more diurnal and if flow reversal occurred during the hours of darkness. The small sample sizes of tagged smolts moving to the lake, and those moving during flow-reversal events, combined with the potential complexity of shifts in diel behaviour through the migration season, indicate that further study of smolt behaviour during diurnally regulated flow releases and linked flow reversal, is needed.

4.3 Context of previous environmental data

The frequency, timing and duration of flow reversal episodes experienced during the study period was typical of recent years. Flow reversal over the period 1 March to 31 May occurred for 281 hours during 2015, the mean flow reversal during the same period between 2006-2014 was 246 hours. Night time reversals are likely to have the most impact on migrating smolts, however this is a relatively rare phenomenon. Night time flow reversal occurred for zero hours in 2015 and 2014, for 4.5 hours during 2013, 6.5 hours during 2012, zero hours during 2008-2011, 16.75 hours during 2007 and 0.25 hours during 2006 (NRW, unpublished data). Thus the level of flow reversal was not atypical during this study, but there was a lack of night time flow reversal which may have helped limit impacts on migrating smolts.

4.4 Conclusion

It is concluded that at sites operating undershot sluices where smolts migrate, including at Bala, upper water column orientated migration routes should be maximized through the structure as this is potentially the main mode of transit smolts are likely to adopt. Such passage routes should be provided where the thalweg hits the structure as this is likely to be the main focus for smolt arrival and this study has demonstrated the importance of the gates in this location. Future research needs to establish the degree to which unusual flow patterns, such as flow reversal may affect smolt behaviour, since during this study there was little overlap in the timing of flow reversal and the main smolt migration, this

occurrence may have been unusual. Further work is also needed to determine the possible cumulative effects on delays at multiple structures on smolt condition and survival to sea and during the early marine phase.

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FIGURES

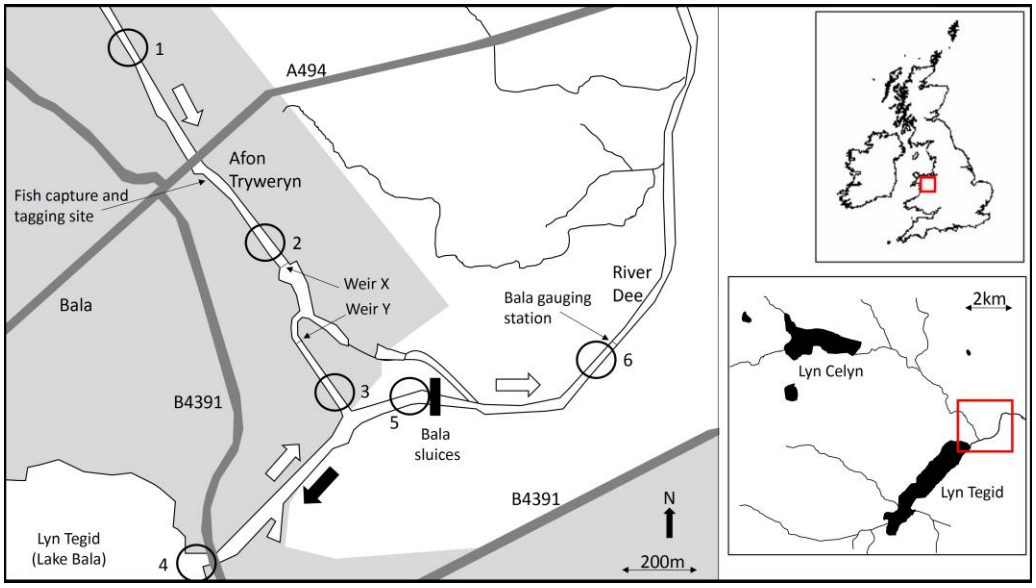

Figure 1. Map of study area. Receiver array locations are denoted by circle symbols numbered 1-6. The fish capture and tagging site, below the A494 road bridge on the Tryweryn and the Bala sluices structure, immediately downstream of array 5, are also marked. Direction of flow through the reach under normal flow scenario is marked as open arrows, and under flow reversal as a solid arrow. The positions of Weir X and Weir Y within the control reach and Bala gauging station are also marked. The left-hand flow bypass downstream of Weir X is only operational during extreme out-of-bank floods, which did not occur in the study.

Figure 2. Bala (Llyn Tegid) sluices, sluice gates are numbered from the left 1, 2, 5, 6 (hidden behind 5), 3 and 4. Photograph taken during springtime water level retention, guillotine gates 1-4 are undershot passage routes and as can be seen gate 5 is lifted clear of the water presenting a central surface orientated passage route.

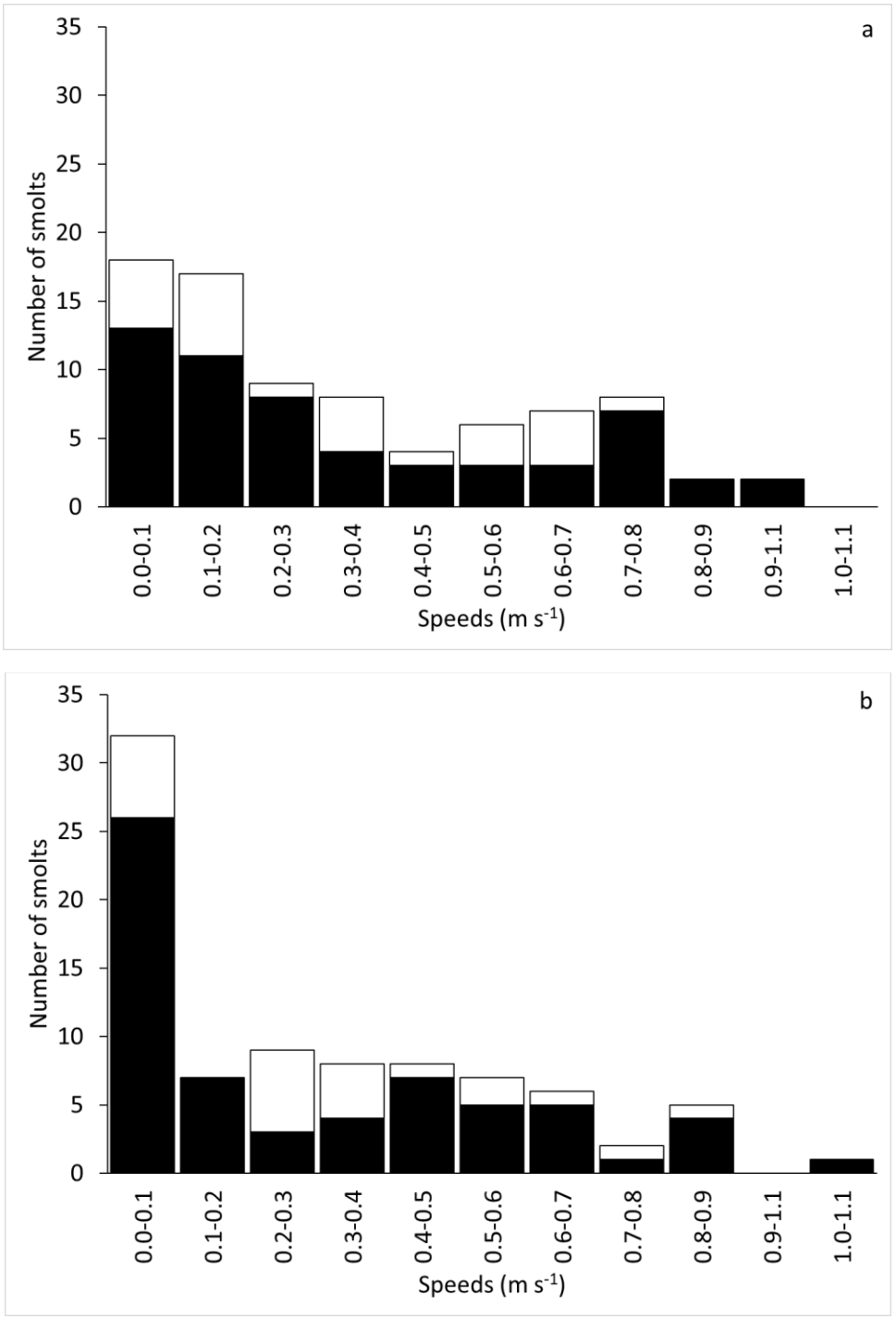

Figure 3. Frequency distribution of the speeds (m s^{-1}) of tracked smolts through the 'control' reach ('a' top) and 'sluice' reach ('b' bottom). Speeds of wild fish are represented by closed (black) bars and speeds of hatchery fish are represented by open (white) bars.

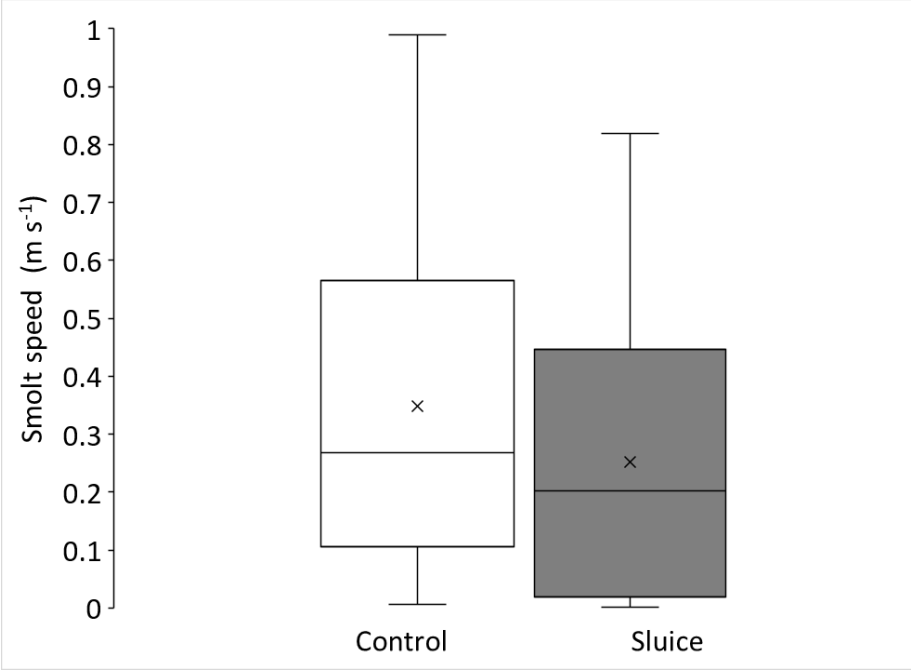

Figure 4. Speeds through control (white) and sluice (grey) reaches for all fish (hatchery and wild, n=75) expressed as box plots with median horizontal lines, mean solid crosses, vertical boxes representing approximately 50% of the observations, whiskers represent the upper and lower 25% of the distribution. Speeds were significantly different (Wilcoxon rank sum test, W = 3561, df = 75, P = 0.013).

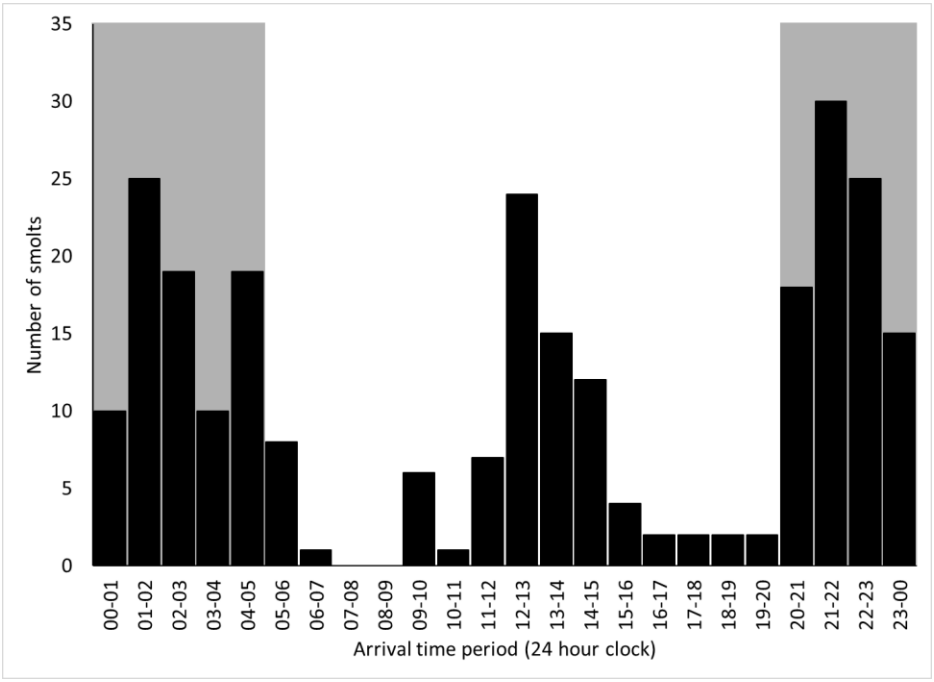

Figure 5. Combined frequency of arrival times of smolts at arrays 3, 5 and 6. Night time periods (20:00-05:00) are represented with a grey shaded background, day time periods (05:00-20:00) are represented with an open white background. Note the apparent avoidance of dawn and dusk.

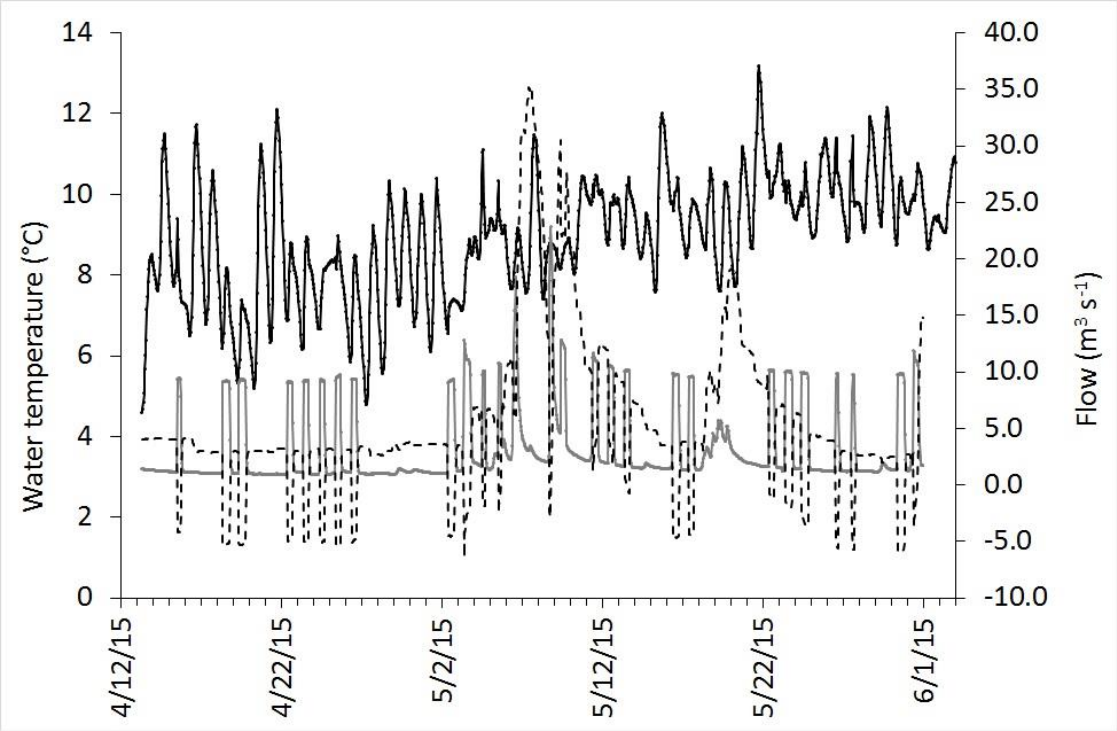

Figure 6. Water temperature (solid black line and markers) plus flow at Weir X (solid grey line and markers) and calculated flow upstream of Bala sluices (broken black line and no markers) with flow reversal events shown as negative values, during the study period. The influence of reservoir releases from Llyn Celyn on arresting daytime warming and flow reversal is clearly evident.